STUDIES ON THE SEXUAL ORGANIZATION OF THE RHIZOCEPHALA. III. THE MODE OF SEX-DETERMINATION IN PELTOGASTERELLA[1]

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All the known Rhizocephala except a few species of the family Sylonidae have been hitherto described as hermaphroditic animals. In the first of this series of papers (Ichikawa and Yanagimachi, 1958) it was reported that *Peltogasterella socialis* Krüger, which had been regarded as one of the representative species of the Rhizocephala, is not a hermaphrodite, but a female fertilized by larval cypris males. A similar sexual organization was demonstrated in *Peltogaster paguri* Rathke and in *Sacculina senta* Boschma (Ichikawa and Yanagimachi, 1960). The sexes of these rhizocephalans are completely separate. The mode of sexual determination in the early stages of *Peltogasterella socialis* Krüger is discussed in this paper.

According to Delage (1884) and Smith (1906), the cypris larvae of *Sacculina* which affix themselves to the host-crabs do not differ morphologically from the larval males that attach around the mantle opening of juvenile parasites. Reinhard (1942) stated that all the cypris larvae of *Peltogaster paguri* are sexually undetermined and undifferentiated. The larvae which attach directly to the host-crabs develop into hermaphrodites. The larvae which fix to the juvenile hermaphrodites become males. Veillet (1943, 1945) reported two kinds of cypris larvae in *Triangulus galatheae* (Syn. *Lernaeodiscus galatheae*) which were considerably different in size. He surmised that the large cypris larvae become hermaphrodites and the smaller cypris larvae function as larval males. According to him, the larger cypris larvae developed from large eggs and the smaller cypris larvae developed from small eggs. Thus, Veillet suggested that the sexes of *Triangulus galatheae* are determined in the egg stage.

In this investigation, it will be reported that the sex of *Peltogasterella*, as the sex of *Triangulus*, is determined at the beginning of development.

MATERIAL AND METHODS

The material used in this investigation was *Peltogasterella gracilis* (Boschma) (syn. *Peltogasterella socialis* Krüger; *cf.* Reischman, 1959) collected from the shore of Oshoro Bay on the west coast of Hokkaido. In this locality the host of this rhizocephalan is almost exclusively the hairy sea-shore hermit crab, *Pagurus lanuginosus* de Haan.

Rearing of the adult and the larvae. It is generally believed that the rearing of the rhizocephalans under laboratory conditions is difficult. However, the author could rear both adult and larval forms of *Peltogasterella* without difficulty. The successful rearing of the adult form was effected by keeping the host-crabs in a healthy environment. The vessels in which the parasitized crabs were kept had a diameter of 15 cm. and a depth of 10 cm. One parasitized crab, after being detached from shell, was placed in each vessel with the level of sea water sufficient to cover the crab. Each vessel was covered with a glass plate to prevent evaporation of the water. Room temperature was not regulated. The crabs and their parasites were not very sensitive to temperature changes. The crabs survived for a long period of time without food. However, it is better to feed them pieces of mussel or clam at intervals. Food debris and the excrements of the crabs were carefully discarded. The sea water in the vessel was renewed at frequent intervals. The females of *Peltogasterella* on the crabs, under favorable conditions, remained alive for about two months. During this period they emitted several batches of nauplius larvae at regular intervals of two weeks (at 20° C.).

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The nauplius larvae emitted from the females were successfully reared in clean sea water when the surface of the water was covered with a film of cetyl alcohol. If the film of alcohol was not employed, a number of larvae adhered to the surface of the water and eventually perished. For the details of the method by which the author succeeded in rearing the larvae, readers are referred to Yanagimachi (1961).

Demonstration of chromosomes of mature eggs. The simple aceto-orcein squash technique was adopted to demonstrate the chromosomes. The procedures were as follows. (1) Detach mature females from the hosts and break the mantle and the wall of ovaries by the use of scissors or needles. (2) Collect the eggs with a pipette and stain them with aceto-orcein for 15 to 30 minutes. The aceto-orcein was prepared according to LaCour (1941). (3) Place the stained eggs on slide with a few drops of aceto-orcein, put a coverslip over the specimens, and blot excess stain away. Squash the stained larvae by exerting careful and controlled pressure on the coverslip. (4) Seal the coverslip with balsam-paraffin (1:1). The preparations thus made remained in perfect condition for months.

RESULTS

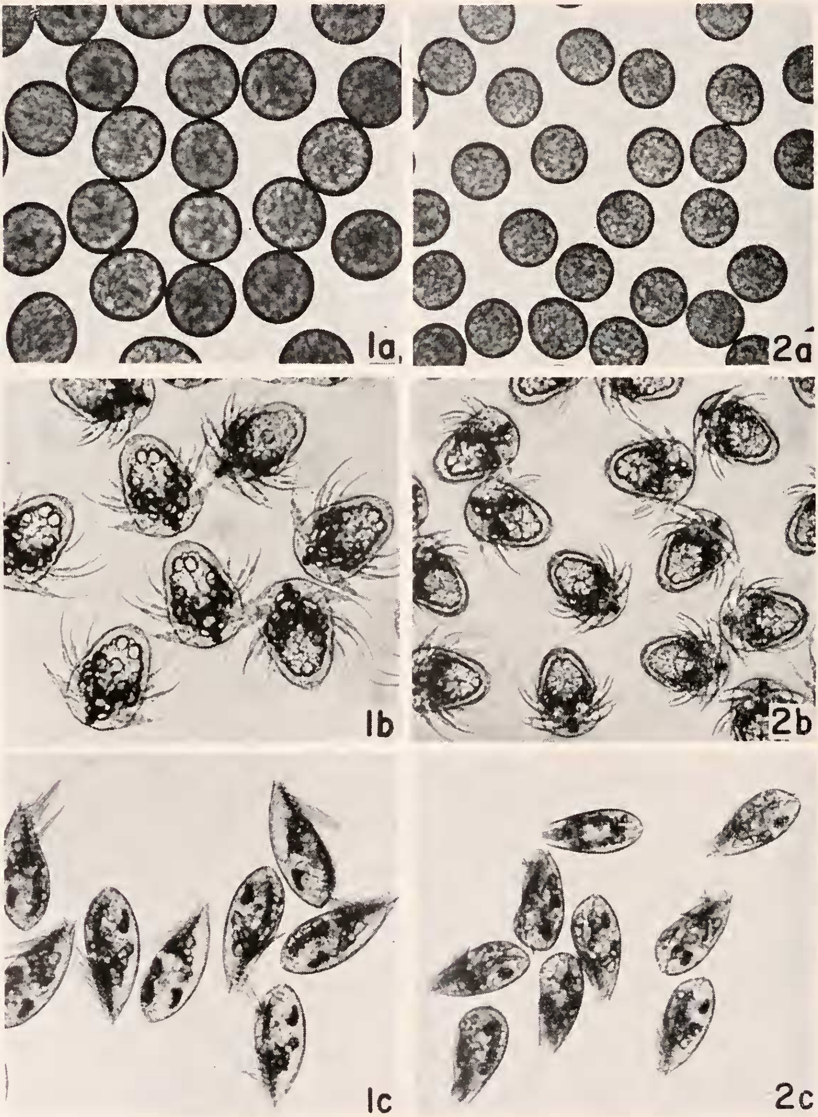
1. *The dimorphism of eggs and larvae*

(a) When a number of adult females of *Peltogasterella* had been reared, all females on some host-crabs produced only large eggs. On the other hand, all females on other host-crabs produced only small eggs. In the maternal mantle cavity (brood pouch), these two types of eggs developed at the same rate and reached the nauplius stage after two weeks (at 20° C.). The large eggs developed into large nauplii, and the small eggs developed into small nauplii. When emitted from the maternal mantle cavity, the nauplii swam actively in sea water and underwent successive moults in 4 to 5 days. The large nauplii metamorphosed into large cypris larvae, and the small nauplii developed into small cypris larvae.

Figures 1 and 2 are photomicrographs of the eggs and larvae of the large and small types derived from the females on two different host-crabs. The measurements of these eggs and larvae are summarized in Figure 3.

The two types of eggs, *viz.,* the large and small eggs, so far as could be ascertained, did not show any distinct structural difference. They differed only in size.

In the nauplius stage, the two types of larvae were identical in structure. They were distinguishable only by their size. In the cypris stage, they were different not only in size but also in structure. The most pronounced structural difference was found in the antennules which function as organs of attachment. Figures 4



FIGURES 1a–c. Eggs and larvae of large type, derived from female *A*. (a) Mature unfertilized eggs. (b) Newly hatched nauplii. (c) Cypris. Magnification: × 55.

FIGURES 2a–c. Eggs and larvae of small type, derived from female *B*. (a) Mature unfertilized eggs. (b) Newly hatched nauplii. (c) Cypris. Magnification: × 55.

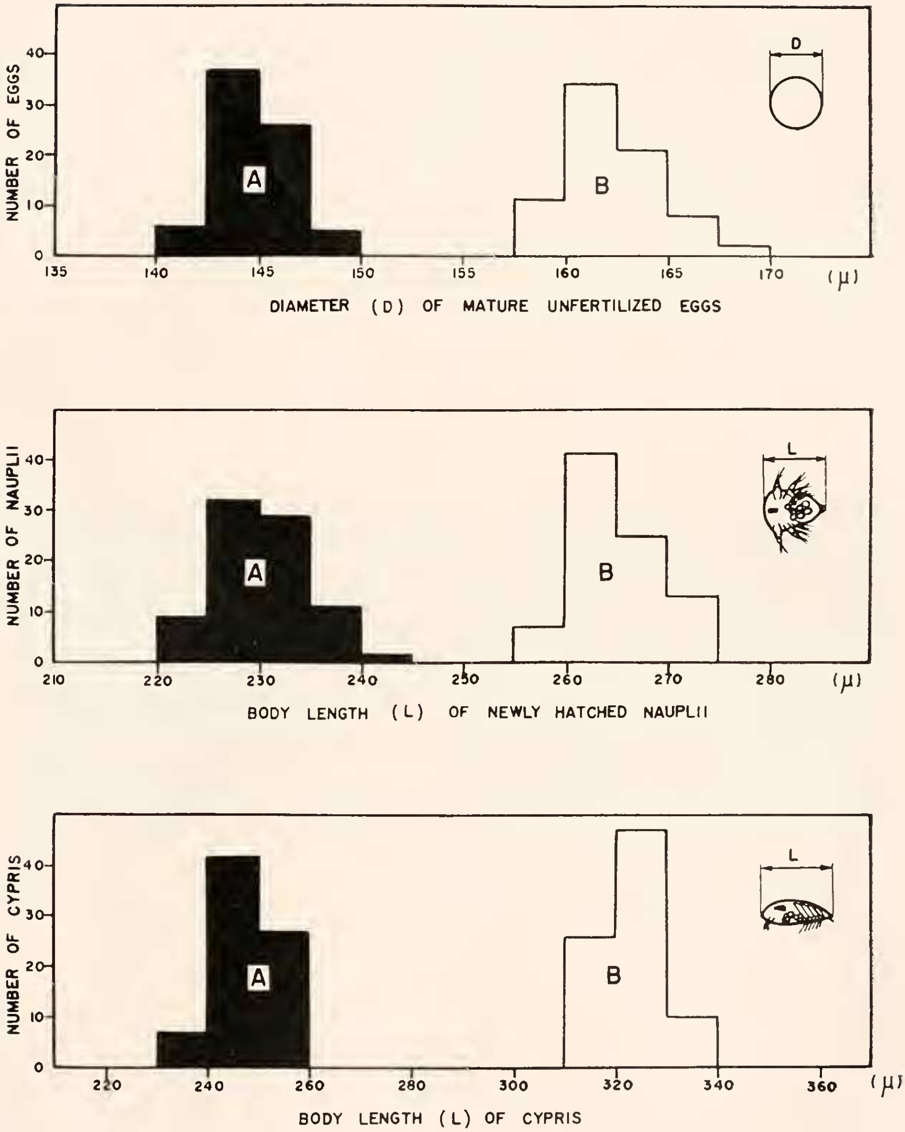


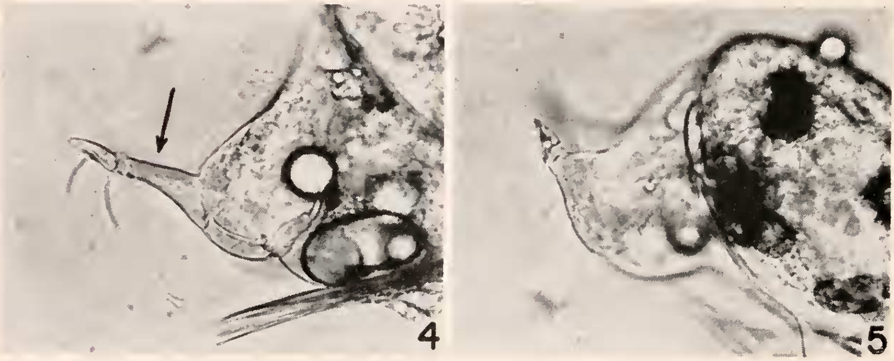
FIGURE 3. Range in size of eggs and larvae derived from two different females, *A* and *B*.

and 5 show the antennules of large and small cypris larvae. The penultimate segment of the antennule of the large cypris is comparatively long and slender (Fig. 4), whilst the corresponding part of the small cypris is greatly diminished or absent (Fig. 5).

(*b*) During its lifetime, an adult female emits several batches of larvae. Experiments were undertaken to know if one female always produces either large or small larvae.

A crab carrying adult females of *Peltogasterella* on its abdomen was placed in a vessel of sea water. All the females except one were mechanically detached. Then, the successive batches of nauplius larvae expelled from this remaining female were examined. Five experiments of this type were conducted. It was found that one female always produces either large or small larvae.

(*c*) *Peltogasterella gracilis,* in common with other species of its genus, occurs gregariously on one host. Do females of *Peltogasterella* on a single host emit both large and small larvae? Table I summarizes the measurements of the larvae and of the eggs derived from the females on six different host-crabs. It may be seen from this table that the females on one host produce larvae of one type—either large or small. The author examined the females on 25 different host-crabs. Females on 11 crabs (2 ♀ and 9 ♂) produced exclusively large larvae and those on 12 other crabs (7 ♀ and 5 ♂) produced small larvae. The females on the remaining two crabs, on the other hand, produced both large and small larvae. The data on these two exceptional females will be presented later.



FIGURES 4 and 5. Comparison of the antennules of the large and small cypris larvae. The cypris larvae were slightly compressed beneath coverslip. (4) Large cypris; an arrow indicates the penultimate segment. (5) Small cypris. Magnification: × 300.

2. *Identification of the sex of larvae*

As has been noted, Veillet (1943, 1945) found large and small larvae in *Triangulus galatheae*. He surmised that the large cypris larvae affix to the body of the host-crabs and develop into hermaphrodites, and that the small ones function as larval males. The present author came to a different conclusion about *Peltogasterella gracilis*. The experiments on which this conclusion is based are here cited.

(*Experiment 1*). On Septemeber 28, 1959, large nauplii were emitted from three females on a host-crab. These larvae were placed in a vessel of sea water and reared. They metamorphosed into large cypris larvae on October 3. On the evening of October 6, two young crabs (*Pagurus lanuginosus* of 3 mm. carapace length) were put into the vessel in which the cypris larvae were actively swimming. At the same time, a large crab (*Pagurus lanuginosus* of 10 mm. carapace length)

TABLE I

Measurements of eggs and larvae derived from Peltogasterella females on six different host-crabs

Host (*Pagurus lanuginosus*)	Parasite (*Peltogasterella gracilis*)					
Sex Carapace length	Individual	Size (length of external sac mm.)	Mean diameter of eggs (μ)*	Range of body length of nauplii (μ)**	Range of body length of cypris larvae (μ) #	Type of cypris # #
Male 6 mm.	a	7	167	265–283	312–329	large
	b	7	163	250–270	312–328	large
	c	7.5	—	—	295–325	large
	d	7	—	—	312–328	large
	e	7	—	257–270	—	—
Male 11 mm.	a	7.5	161	256–276	312–336	large
	b	7	—	—	295–315	large
	c	7	—	—	312–325	large
	d	6.5	—	—	312–320	large
	e	7	—	—	311–332	large
Male 15 mm.	a	5	170	260–274	309–330	large
	b	5	168	263–268	312–329	large
	c	6	173	—	311–329	large
	d	6	—	—	312–329	large
	e	4	—	260–290	295–320	large
	f	5	—	260–276	—	—
Female 12 mm.	a	6.5	143	225–242	242–260	small
	b	7	140	219–240	225–245	small
	c	7	—	225–242	230–252	small
	d	6	—	225–242	—	—
Male 13 mm.	a	9	144	222–243	242–260	small
	b	8	140	212–234	242–250	small
	c	8.5	—	210–235	250–275	small
	d	8	—	—	242–260	small
	e	9	—	—	234–260	small
	f	6	—	—	235–255	small
Female 13 mm.	a	7.5	142	216–242	242–260	small
	b	7	145	220–240	234–256	small
	c	7	—	—	234–260	small
	d	6.5	—	207–225	—	—
	e	7	—	219–230	—	—

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* Mature unfertilized eggs which had just been released from the ovary into mantle cavity (brood pouch) were measured. The measurement was made on about 50 eggs.

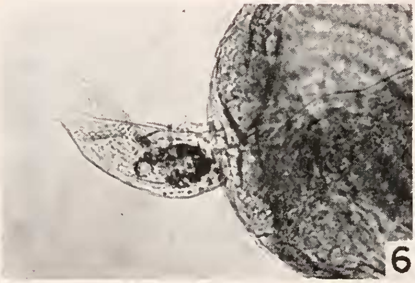
** The measurement was made on 30–50 newly hatched nauplii which had not yet undergone their first moulting. The body length means the distance between the frontal margin of the carapace and the tip of the caudal spine.

The measurement was made on 30–50 recently metamorphosed cypris larvae. The body length means the distance between the anterior and the posterior ends of the carapace.

Types of cypris larvae were identified by measuring the body size and examining the structure of antennules.

carrying juvenile females of *Peltogasterella* on its abdomen was placed in the same vessel. The number of juvenile females on the crab was 15, and they varied from 2.5 to 3 mm. in length of the external sac-like portion. In every respect they were identical to those females which had recently emerged from the crab's abdomen. On the next morning, the three crabs were removed from the vessel and examined under a binocular dissecting microscope. Five cypris larvae were found attached to the mantle opening of four juvenile females of *Peltogasterella.* Two cypris larvae were about to inject their internal cellular contents into the mantle cavity of the juveniles (Fig. 6). Three cypris larvae, on the other hand, had already injected their cellular contents into the juveniles. No cypris was detected on the surface of the crab's body, although careful and repeated examinations were carried out.

(*Experiment 2*). On October 1, small nauplii were discharged from five females on a host-crab. They were placed in a vessel of sea water and reared. On October 5, they metamorphosed into small cypris larvae. On the evening of October 7, two young crabs (*Pagurus lanuginosus* of 3 to 4 mm. carapace length) were put into the vessel in which the small cypris larvae were swimming. At the same time, a large crab (*Pagurus lanuginosus* of 13 mm. carapace length), infested by 13 juvenile females of *Peltogasterella,* was put into the vessel. The next morning, the three crabs were removed from the vessel. On careful examination, several cypris larvae were found attached to the body of the young crabs. These cypris larvae were invariably affixed to the base of the setae on the crab's body. The setae on the carapace were the most frequent site of fixation (Fig. 7). No cypris was found at the mantle opening of the juvenile females of *Peltogasterella.*



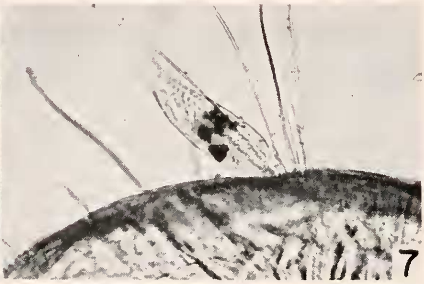


FIGURE 6. A large cypris fixed at the mantle opening of a juvenile female. Magnification: × 80.

FIGURE 7. A small cypris fixed at the base of a seta on the carapace of a host-crab. Magnification: × 80.

Fifteen experiments of these types have been conducted, with the result that the large cypris larvae always attach to the mantle opening of the juvenile females of *Peltogasterella* and never fix on the body of the host-crab. The small cypris larvae search for the host-crabs and affix at the base of setae, without being attracted to the juvenile females. From these facts it is concluded that the cypris larvae of the small type are prospective females and those of the large type function as larval males.

3. *Morphological distinction in the male-producing and female-producing females*

As stated in the first section, the females of *Peltogasterella* on one host usually produce larvae of the same type, *i.e.,* either large or small larvae. From the results of the experiments described, it is now certain that the larvae of small type are prospective females while those of large type function as males. Then, it may be said that the females on a host are regularly "female-producing" or "male-producing."

Now, a question arises as to whether the female-producing and the male-producing females are morphologically different. A number of living specimens of both female-producing and male-producing adult females were examined to obtain the answer to this question. The external appearance of the sac-like portion, the position of the stalk, the site and the shape of the colleteric glands, and the structure of the mantle opening were compared, but no distinct difference was detected. Some specimens of the female-producing and the male-producing females were cut in serial sections and examined. No discernible difference in structure of various organs of the two types of the adult females was detected. The observations of the author reveal no evident morphological difference between the male-producing and the female-producing females.

4. *The differences in the chromosomes of the male-producing and the female-producing eggs*

The eggs of *Peltogasterella* begin maturation division while they are still in the ovary. Having reached the stage of the first maturation division metaphase, the eggs are expelled through the colleteric glands into the mantle cavity of the female. The first maturation spindle then passes into telophase and the first polar body is extruded, the second polar body being immediately formed without reconstruction of the nucleus. The penetration of the sperm into the egg occurs immediately before the second polar body is extruded (Shirase and Yanagimachi, 1957).

When the author examined the metaphase plate of the first maturation division of the large male-producing eggs, 15 bivalent chromosomes were observed (Figs. 8 and 9). In the anaphase of this division, these chromosomes segregated equally and passed into the two poles (Figs. 10 and 11). In the metaphase plate of the second maturation division, 15 univalent chromosomes were counted.[3]

The chromosomal arrangements were different in the small female-producing eggs. In the metaphase plate of the first maturation division, a univalent chromosome was always found with 15 bivalent chromosomes (Figs. 12 and 13). This chromosome showed a peculiar behavior at the later stage of the first maturation division. It remained in the middle of the spindle after the other chromosomes had passed to the pole (Figs. 14–16). It was greatly stretched in the axis of the spindle and had the appearance of a body under considerable tension. In most cases it showed a conspicuous longitudinal split which was so distinct that the halves resembled two parallel lagging chromosomes. Only in the late anaphase of the division did this peculiar univalent chromosome pass to one pole of the spindle (Figs. 17–22). In the metaphase plates of the second maturation division

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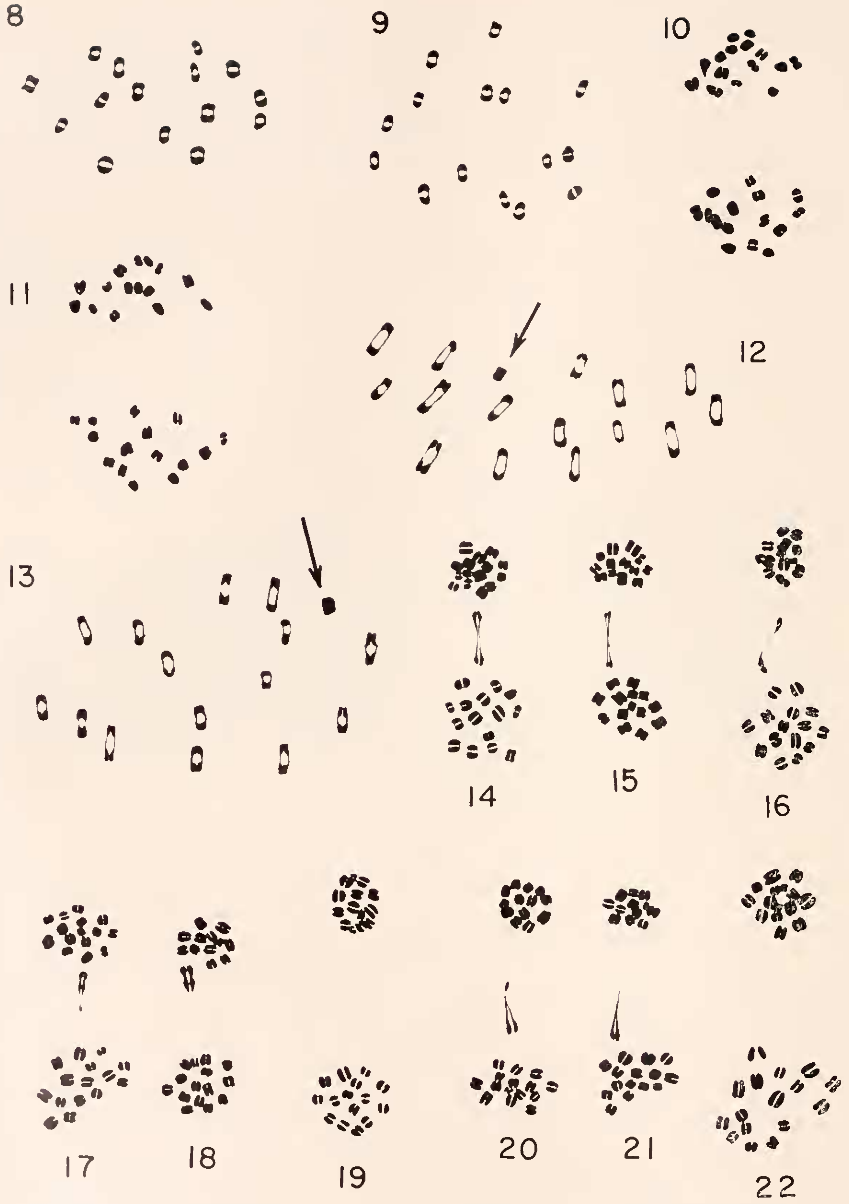
[3] Thirty to forty chromosome counts have been made for each of the represented stages.



FIGURES 8–22. Chromosomes of the large and the small eggs. Magnification: × 1500. Camera-lucida drawings.

FIGURES 8–9. Chromosomes of the first maturation division metaphase of the large male-producing egg.

FIGURES 10–11. Chromosomes of the first maturation division anaphase of the large male-producing egg.

FIGURES 12–13. Chromosomes of the first maturation division metaphase of the small female-producing egg. A univalent chromosome (indicated by an arrow) is found beside 15 bivalent chromosomes.

15 and 16 univalent chromosomes were counted. No lagging chromosomes were detected in the course of second maturation division.

5. *On a few exceptional females*

Of 25 parasitized crabs that the author reared, two were found to bear unusual females which produced both large and small larvae. The data concerning these females are here presented.

(*a*) *Five females on a host-crab* (♀) *of 12 mm. carapace length.* All of these females measured from 8.5 to 9.5 mm. in length of the external sac-like portion. One of these emitted a batch of nauplius larvae on October 10. When these nauplii were measured immediately after hatching, 90% of them had a body length of 225 to 240 μ. The remaining 10% of the larvae, on the other hand, measured from 250 to 260 μ in length. Thus, the nauplii emitted from this female consisted of many small larvae and a small number of large larvae. When these larvae were reared, small nauplii metamorphosed into typical small cypris larvae (240–270 μ) and large nauplii developed into large cypris larvae (280–295 μ). The four other females on the same host emitted numerous nauplii on October 10 and 11. In this case, each female also emitted many small larvae and relatively few large forms. The results of experiments showed that small larvae were destined to become females. Unfortunately, it was not ascertained whether the large larvae were functional male individuals, owing to the small number of the larvae.

(*b*) *Two females on a host-crab* (♂) *of 13 mm. carapace length.* There were 7 females on this host-crab. They measured 7 to 8 mm. in length. Five of them produced exclusively large nauplii which developed into large cypris larvae. The other two females produced both large and small nauplii which developed into large and small cypris larvae, respectively. In this case, the larger larvae were more numerous than the smaller ones.

The chromosomal constitution of the exceptional females described above was examined. It was found that the females which produced many small and few large larvae contained in their ovary oöcytes with 15 bivalent chromosomes and a univalent chromosome (the first maturation division metaphase was examined), while the females that produced many large and few small larvae had oöcytes with 15 bivalent chromosomes. Thus, the exceptional females in question were typical female-producing and male-producing females, so far as their chromosomal constitutions are concerned. Why did these females produce both large and small larvae? Although some tentative explanations might be presented here, the author would like to dismiss them until incontestable evidence is obtained.

REMARKS

According to Veillet (1943, 1945), the cypris larvae of *Triangulus galatheae* fall into two groups, the large cypris and the small cypris larvae. Although lacking direct evidence, Veillet maintained that a large cypris develops into an adult

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FIGURES 14–16. Chromosomes of the first maturation division anaphase of the small female-producing egg. A lengthened univalent chromosome is in the middle of the anaphase spindle.

FIGURES 17–22. Late anaphase of the first maturation division of the small female-producing egg. The univalent chromosome passes to polar body (17–19) or to egg nucleus (20–22).

hermaphrodite, while the smaller one functions as a larval male. In *Sacculina carcini,* according to Veillet, there is no larval dimorphism, but he conjectured that there might be two physiologically different kinds of cypris larvae, one a prospective adult hermaphrodite and the other the larval male. In *Peltogasterella gracilis*, as has been elucidated by the present study, there occurs a marked larval dimorphism. In this species, the large cypris represents the male sex and the small one represents the female sex. A notable fact is that an adult female rarely produces both male and female larvae. It produces regularly either male larvae or female larvae. In *Peltogasterella sulcata* (syn. *Gemmosaccus sulcatus; cf.* Reischman, 1959), Veillet (1952) observed that the cypris larvae derived from adult parasites on a host-crab (*Pagurus cuanensis*) successfully fixed to the crab, while those which were derived from the parasites on two other host-crabs (*P. cuanensis*) failed to fix upon the crab. Veillet made no mention of the reason for such facts. The present author surmises that the cypris larvae derived from the parasites on the one host-crab were female larvae and those from the parasites on the other two crabs were male larvae. The male larvae do not fix to the host-crab.

As examples of animals which are known to have the male-producing and the female-producing females in their population, the aphids (*Aphis* and *Phylloxera*) and the gall-fly (*Neuroteus*) may be mentioned (Morgan, 1912, 1915; Doncaster, 1916). In *Phylloxera caryaecaulis*, Morgan (1912, 1915) found that the eggs which are laid by the female-producing females, *viz.*, the female-producing eggs, are larger than those which are laid by the male-producing female, *viz.*, the male-producing eggs. Morgan observed that during the maturation division of the small male-producing egg two X-chromosomes lag behind the others in the spindle during anaphase, fail to enter the egg nucleus, and pass to the polar body. In the large female-producing egg no elimination of the X-chromosomes occurs. The fate of the egg (whether it develops into a female or into a male) is determined long before maturation division occurs. Why the oöcytes with the same chromosomal constitution develop into two different types of eggs has not yet been settled, although a hypothesis was formulated by Morgan (1915).

As another example of the animal which lays two morphologically and sexually different kinds of eggs, mention may be made of *Dinophilus apatris* (Archiannelida). Here, a female produces both large and small eggs which develop into females and males, respectively. The eggs are laid in a cocoon. The ratio of the large female-producing eggs to the small male-producing eggs is not always 1 : 1, but it varies with females and under influence of external conditions (Korschelt, 1882; Nachtsheim, 1919; Tzonis, 1938). The reason why the same female produces two different kinds of eggs is not yet fully understood. No cytologically distinguishable sex-chromosome has been demonstrated. In *Peltogasterella gracilis* there exists a special chromosome which behaves like a sex-chromosome. The female-producing female possesses this chromosome, while the male-producing female does not. The exact nature and function of this chromosome is unknown, and must be the subject of future research.

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SUMMARY

1. The adult females of the rhizocephalan, *Peltogasterella gracilis* (Boschma), although they appear similar, are in reality two kinds, large-egg-producing and small-egg-producing females.

2. The large eggs develop into large larvae which function as males (larval cypris males). The small eggs develop into small larvae which give rise to adult females.

3. In the metaphase plate of the first maturation division of the large male-producing egg 15 bivalent chromosomes are seen, while in the small female-producing egg a univalent chromosome is found beside 15 bivalent chromosomes.

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